THE RESPONSE OF A KANSAS WINTER BIRD COMMUNITY TO WEATHER, PHOTOPERIOD, AND YEAR

MARTIN A. STAPANIAN,[1,4] CHRISTOPHER C. SMITH,[2,5] AND ELMER J. FINCK[3]

ABSTRACT.—We conducted a bird census along the same route nearly each week for 14 winters (194 censuses), and compared the mean number of species per station and the total number of species recorded on the census with the length of photoperiod and weather variables. We found significant differences among winters for both indicators of species richness. This result is consistent with previous studies in which abundance of food was measured in the same general area. Both indicators of species richness were negatively associated with the number of days after 1 November. This result is consistent with the hypothesis that wintering species dependent on nonrenewed food resources lose individuals to mortality or emigration. Further, there was a positive relationship between photoperiod and both indicators of species richness. This result is consistent with the hypothesis that the detection of individuals in the early morning hours increases with the amount of daylight they have available for foraging and social behaviors. Wind speed and temperature had negative and positive relationships, respectively, to species richness. The number of species per station was greatest on days when the ground was covered with dew and least on days when snow depth was more than 15 cm. When the "winters" were divided into four 30-day "quarters", most of the 61 species were recorded with equal frequency in each quarter. Eight species were detected less frequently at the end of winter than in the beginning. Four species exhibited the reverse pattern. Two species were recorded more frequently at the beginning and at the end of the winter than during the middle. Temperature, wind, photoperiod, successive winter day, year, and species-specific evolutionary history all affect winter bird species richness. *Received 1 Oct. 1998, accepted 5 August 1999.*

Winter is a stressful season of the year for endotherms at mid- and high latitudes. Severe cold, short photoperiod, and a mostly nonrenewed food supply make it a challenge to maintain a constant body temperature. Many bird species migrate to more hospitable climates. For those species that overwinter at higher latitudes, weather conditions have been shown to affect the amount of body fat stored (White and West 1977, Dawson and Marsh 1986, Peach et al. 1992, Waite 1992, Houston and McNamara 1993, Rogers et al. 1994, Pilastro et al. 1995). Collins (1989) provided a short review on some of the major physiological adaptations in birds for surviving the winter. Robbins (1972, 1981a) and Altman (1983) discussed the importance of weather conditions on winter bird populations.

Although detailed, long-term winter studies exist for specific species (Loery and Nichols 1985), data for studies of overwintering bird communities often are collected only for a few days per year (cf., Erskine 1992). For example, three counts per year are made for the Finnish winter bird census routes (Hildén 1987), and the Christmas Bird Count is an annual one-day count of an area. The daily effects of weather components and the annual effects of available food resources (e.g., mast crop failure) on the number of species in an area are often difficult to determine or are statistically confounded. Instructions for the Winter Bird-Population Study (Robbins 1981b) call for a minimum of six visits per site per year. However, daily weather data for the study sites and analyses of the effects of weather components on species richness are typically lacking (Robbins 1981a). Further, depending on species-specific responses to abiotic factors and food abundance, bird species may differ in their detectability during the course of winter.

We analyzed data from bird censuses conducted at nearly weekly intervals for 14 years (194 censuses) along the same route. We include in our analyses weather data collected from a permanent station approximately 10 km from the route. Our objectives were to (1) quantify the effects of weather components, photoperiod, and the cumulative number of

[1] Ohio Cooperative Fish and Wildlife Research Unit, The Ohio State Univ., 1735 Neil Ave., Columbus, OH 43210.
[2] Division of Biology, Ackert Hall, Kansas State Univ., Manhattan, KS 66506.
[3] Division of Biological Sciences, Box 4050, Emporia State Univ., Emporia, KS 66801.
[4] Present address: USGS/BRD, Lake Erie Biological Station, 6100 Columbus Ave., Sandusky, OH 44870.
[5] Corresponding author: E-mail: cccsmith@ksu.edu

winter days on species richness; and (2) to determine if the frequency of detection of individual species changed over the course of the winter. To accomplish the first objective, we used a statistical procedure that accounts for the correlation structure (i.e., time-dependency) between censuses taken within each winter. We accomplished the second objective by testing the null hypothesis that individual species were recorded with equal frequency within each of four 30-day intervals during the winter.

METHODS

Census route and field method.—Our study, like others based on seeing and/or hearing birds to count their presence, measured the visual and auditory detectability of birds. Birds were counted with a modified Breeding Bird Survey procedure (Robbins et al. 1986) along a regular census route across the border between Riley and Pottawatomie counties, Kansas (Stapanian 1982, Stapanian et al. 1994). The route consisted of 16 stations; unlike the Breeding Bird Survey routes, the stations were not separated by regular 0.81 km intervals. Instead, stations were selected to represent typical upland and riparian forest habitats with some tree species bearing fleshy, bird-dispersed fruit in proportion to their presence in the Kansas Flint Hills. Nine stations were along one road and seven were along another. There were eight convenient sequences in which the 16 stations could be visited. Each of the eight sequences of stations was used during eight consecutive censuses. Therefore, there was no consistent pattern in the time after official sunrise that each station was visited. Distances between stations on the same road ranged from 0.3 to 1.6 km (mean = 1.0). The nearest stations on the two roads were separated by 13 km. Because our goal was to quantify the effects of weather, photoperiod, and cumulative number of winter days on species richness in the entire area, data were pooled for all stations. Birds were identified to species, and the number of individuals was counted for 3 min at each station. Birds flying overhead were included in the analysis. Censuses were conducted at approximately weekly intervals November–February, 1982–1996. Each census began within 1 h after sunrise and required approximately 2 h to complete. In accordance with instructions for Breeding Bird Surveys (Robbins 1981b), no censuses were conducted in fog, steady drizzle, prolonged rain, or winds stronger than Beaufort 3 (13–19 km/h).

In selecting stations for the census, the original criterion was a wooded area with concentrations of trees of *Juniperus virginiana, Morus rubra,* or *Celtis occidentalis* that would attract frugivorous birds (Stapanian 1982). The two roads along which the stations were spaced held a variety of habitats (Table 1), which affected our bird censuses. At each station we visualized a line perpendicular to the road and classified each of

TABLE 1. Habitat type for census stops by the number of stops at which the habitat was represented and by the number of 90° arcs at the 16 stops that were predominantly composed of that habitat.

Habitat	Number of census stops	Number of 90° arcs
Native prairie	1	1
C₃ grass pastures	5	6
Row crops	7	13
Residential and farm buildings	7	9
Dense shrub	2	4
Juniper forest	4	4
Young mixed forest	7	12
Mature mixed forest with oak	3	6
Mature mixed forest without oak	2	6
Riparian margin forest	2	3
Forest beyond crops	5	—

the four 90° sections thus formed as being predominantly in one category for Table 1. Thus, there are a total of 64 sections for the 16 stations that form Table 1. The Flint Hills area of Kansas held almost no forests before European settlement (Axelrod 1985). Only about 16 species of native trees have spread into the area from the eastern deciduous forests after the control of prairie fires. Two stations were completely surrounded by forest, but 14 stations had at least one 90° section of forest holding one of the three tree species producing fleshy fruit and the other two stations had fence rows with *M. rubra.* The mature forests are separated into those with and without bur oaks (*Quercus macrocarpa*) because this tree species must have a large acorn crop in order for Red-headed Woodpeckers (*Melanerpes erythrocephalus*) to winter in the area. Some of the residences near stations on the census were homes with lawns while others had corrals for livestock. At five stations birds could be heard calling from mature forests beyond extensive fields of row crops (Table 1).

Although our survey has been conducted along the same route nearly every week since 1978 (Stapanian et al. 1994), because weather data are not available before 1982, we only analyzed data from November 1982 through February 1996. We selected the period between 1 November through 28 February because it represents a time interval in the study area during which (1) food sources are not renewed and (2) Neotropical migrants are rarely present. We divided this interval into four 30-day periods (quarters) for analysis of the presence of individual species. Our censuses were designed to monitor populations of upland birds (Stapanian 1982, Stapanian et al. 1994). Aquatic and nocturnal species were eliminated from the present analysis. For each census, we calculated the mean number of species recorded per station and the total number of species recorded from all stations.

Our procedures differed from Breeding Bird Surveys in three ways. First, when no birds were evident

at a station, we spished to attract them. Second, when we were unable to find new birds where the car was parked, we walked along the road in search of birds. Third, we had more than one observer on 58% of the censuses. Neither of the first two differences biased the data. Making noise and walking along the road when no birds were evident would tend to overestimate the number of bird species and individuals when they were lowest. Thus, any conclusions we would make about which factors decreased bird activity and the number of species would be conservative. The number of observers ranged from one (82 censuses, 42.1%) to four (3 censuses, 1.5%). The number of censuses in which there were two and three observers were 81 (41.5%) and 29 (14.9%), respectively. In exploratory analyses, we found that the number of species recorded was greater when more than one observer participated in the census. Therefore, we adjusted mean species per station and total species per census for the number of observers. In controlled experiments performed during winter on this route (C. C. Smith, unpubl. data), we found that the mean number of species per station and total species per census increased on average by factors of 1.32 and 1.08, respectively, for multiple observers over those values found by one observer. Thus, when the number of observers was greater than 1, we divided mean species per station and total species per census by 1.32 and 1.08, respectively. Further, C.C.S. participated in all censuses and his hearing still allows him to detect a Brown Creeper (*Certhia americana*) at 30 m. E.J.F. participated in almost all censuses from 1982 through February 1989. J. Cavitt, S. Hansen, S. Hull, C. Pacey, G. Radke, and C. Rebar participated in at least four censuses each.

Weather data.—Weather data for each census were collected automatically from a permanent station at the Konza Prairie Research Natural Area, located within 18 km from all our census stations. The weather station measured wind speed at hourly intervals on the hour. We, therefore, selected weather data recorded at 07:00 on each census day. Because each census began within 1 h after official sunrise, 07:00 does not represent a standard time relative to sunrise for all censuses. However, we were confident that the data were representative of the weather during our censuses.

We use a standard weather service formula to convert temperature and wind speed to a wind chill temperature. Wind chill temperature exceeded air temperature only for wind speeds greater than 6.7 km/h, which occurred on only six censuses. In exploratory analyses of variance, we found that of the weather variables recorded, only temperature and wind speed accounted for a significant proportion of the variance in our statistical models.

We ranked ground conditions from 1 though 6 according to what we perceived as increased difficulty for birds in finding food on the ground: (1) dry, (2) dew, (3) frost, (4) wet from rain or melting snow, (5) snow 15 cm or less deep, and (6) snow more than 15 cm deep. Ground condition was recorded at the first station we visited on all but six censuses. All stations were then assigned the same weather data and ground condition class as the first station for the census.

Statistical analyses.—"Winter day" was designated as the number of days after 31 October for each census. Photoperiod was calculated from published tables (U.S. Naval Observatory 1945) as the number of minutes between official sunrise and official sunset on each census date, and ranged from 565 to 679 min.

We tested for the effects of winter day, photoperiod, and weather components on our two indicators of species richness. In exploratory analyses and previous studies (Stapanian et al. 1994) we found considerable variance in the species richness among winters. Further, we found significant time dependency among the successive censuses within winters. Therefore, we used a mixed models procedure (Crowder and Hand 1990, SAS Institute 1992, Littell et al. 1996) in which each winter was treated as a random effect (i.e., whole plot), and the remaining variables were treated as fixed covariates (i.e., subplots) to account for the correlation structure among the censuses within winters. The degrees of freedom and mean squares were adjusted for time dependency based on the covariance structure and inference space. Ecologically, this meant that we removed winters as a random effect from the statistical model tests for the effects of the fixed covariates based on an average set of conditions at the beginning of winter. The resulting model was general, not winter-specific.

We evaluated the covariance structure in three ways: (1) uniform correlation (compound symmetry), (2) exponentially decaying, and (3) Markov chain. In exploratory analyses, we found that the uniform correlation method best represented the covariance structure of the data set. Further, we found that none of the two-way interactions between the fixed covariates contributed significantly to the models ($P > 0.05$ in all cases). Thus, we performed the mixed models analyses only on the main effects of the fixed covariates. We performed Tukey's tests for *a posteriori* testing on the effects of specific ground condition classes on diversity.

We defined ordinal year as the ordinal number of a census year (i.e., year 1 = 1982–1983, year 2 = 1983–1984, . . . , year 14 = 1995–1996). We performed standard Pearson correlations between ordinal year, species richness, and our weather variables. In this manner, we were able to test for overall temporal trends in weather and diversity on census days on our census route.

For each species, we calculated the proportion of the censuses conducted in each quarter (30-day interval) of each year in which that species was recorded (Appendix). These quarterly proportions were then pooled across all 14 winters for each species. Using analysis of variance, we then tested the null hypothesis that each species was recorded in equal proportions in all four quarters. Tukey's pair-wise comparisons were used for all *a posteriori* testing. SAS for Personal Computers, version 6.12 for Windows was used for statistical computations.

TABLE 2. Summary statistics for each winter for the total number of species recorded on each census and the mean number of species per station on each census. These variables were adjusted for number of observers. Years that share a grouping letter were not significantly different (Tukey's pair-wise comparisons, $P > 0.05$) for that indicator of diversity.

Year	n^a	Species per census		Species per station	
		Mean	SD[b]	Mean	SD[b]
1982–1983	12	24.18	2.29 B, C, D	5.00	0.74 A, B, C
1983–1984	14	18.21	4.97 E	3.52	1.54 D, E
1984–1985	14	19.48	2.65 D, E	3.99	1.02 C, D
1985–1986	13	23.40	3.32 B, C	5.04	1.44 A, B, C
1986–1987	11	22.09	3.67 B, C, D, E	4.89	1.02 A, B, C, D
1987–1988	12	23.73	2.59 B, C	5.50	1.18 A, B
1988–1989	14	24.45	2.07 B, C	5.37	0.91 A, B
1989–1990	15	23.75	4.16 B, C	4.98	0.59 A, B, C
1990–1991	14	25.93	2.76 B	5.86	1.09 A
1991–1992	15	18.39	3.26 E	3.65	1.25 D
1992–1993	15	23.71	2.99 B, C	4.97	1.07 A, B, C
1993–1994	16	29.81	3.67 A	5.36	1.12 A, B
1994–1995	13	24.00	2.16 B, C	5.34	1.36 A, B
1995–1996	16	22.32	1.37 C, D	4.63	0.95 B, C, D

[a] n = number of censuses.
[b] SD = standard deviation.

RESULTS

There were significant differences among winters for the annual means of both total species per census and species per station ($F_{13,180}$ = 13.87 and 5.46, respectively, $P < 0.001$ in both cases; Table 2). Consequently, we treated winters as random effects in our mixed model analysis. The results from the mixed model procedure (Table 3) suggested significant effects from winter day, photoperiod, temperature, and wind speed for the number of species per census and species per station. Temperature and photoperiod were positively related to both indicators of species richness when the covariance structure was taken into account (slopes in Table 3). On the other hand, wind speed and winter day had negative effects on both indicators of diversity (slopes in Table 3).

On average, a change of 1° C in temperature or 1 km/h in wind speed had a greater effect on species richness than did either a change of 1 min in photoperiod or 1 day further into winter.

Ground condition had a significant effect on species per station, but not on species per census in the mixed model analyses (Table 3). Values of species per station were lowest when there was more than 15 cm of snow on the ground and greatest when the ground was covered with dew (Table 4).

Both of our indicators of species richness increased over the course of our study. There was weak but positive correlation between species per census and ordinal year ($r = 0.27$, df = 12, $P < 0.001$) and between species per station and ordinal year ($r = 0.15$, df = 12,

TABLE 3. Results of the mixed models ANOVA procedure. Two-way interactions were not found to be significant in exploratory analyses ($P > 0.05$). Slopes and standard errors (SE) of the slopes are not reported for ground condition because it was not a continuous variable.

Source	df	Species per census				Species per station			
		F	$P > F$	Slope	SE	F	$P > F$	Slope	SE
Winter day (days)	1	20.35	0.001	−0.033	0.007	21.89	0.0001	−0.011	0.002
Photoperiod (minutes)	1	11.51	0.0009	0.029	0.008	40.03	0.0001	0.017	0.003
Temperature (° C)	1	7.65	0.0063	0.111	0.040	30.53	0.0001	0.070	0.013
Wind speed (km/h)	1	26.36	0.0001	−0.634	0.123	45.86	0.0001	−0.264	0.039
Ground condition	5	1.10	0.3636			2.54	0.0301		

TABLE 4. *A posteriori* tests (Tukey's pair-wise comparisons) on the effects of ground condition on the mean values of the mean number of species per station on a census. Means of ground condition classes with at least one letter in common are not significantly different ($P > 0.05$).

Ground condition	Class	n[a]	Mean of mean species per station
Clear, dry	1	53	4.93 B
Dew	2	10	6.12 A
Frost	3	39	5.14 B
Wet	4	31	4.75 B
Snow ≤ 15 cm	5	50	4.47 B
Snow > 15 cm	6	5	3.56 C

[a] n = number of censuses.

$P = 0.035$). Further, there was a weak but negative correlation between wind speed and ordinal year ($r = -0.16$, df = 12, $P = 0.022$), which suggested that wind speed on census trips decreased over the course of this study. We made no conscious change in our policy of when to hold censuses during our study that would have resulted in lower wind speeds during censuses. Neither temperature nor ground condition class was significantly correlated with ordinal year ($P > 0.05$ in both cases).

Sixty-one species were recorded for our study (Appendix). Only two species, American Crow (*Corvus brachyrhynchos*) and Black-capped Chickadee (*Poecile atricapillus*), were recorded on all 194 censuses. Twenty-two species (36.1% of the total species) were recorded on at least 50% of the censuses. Thirteen species (21.3% of the total species) were seen on less than 5% of the censuses. There was no consistent pattern to the temporal occurrences of individual species (Appendix). For most species, the proportion of the censuses in which they were recorded was the same for each quarter. Eight species, Northern Flicker (*Colaptes auratus*), Golden-crowned Kinglet (*Regulus satrapa*), Northern Bobwhite (*Colinus virginianus*), White-crowned Sparrow (*Zonotrichia leucophrys*), Common Grackle (*Quiscalus quiscula*), Field Sparrow (*Spizella pusilla*), White-throated Sparrow (*Zonotrichia albicollis*), and Lincoln's Sparrow (*Melospiza lincolnii*), occurred more frequently in early winter than in late winter. The reverse trend was exhibited by four species, American Tree Sparrow (*Spizella*

arborea), Tufted Titmouse (*Baeolophus bicolor*), Western Meadowlark (*Sturnella neglecta*), and Eastern Meadowlark (*Sturnella magna*). Two species, Red-winged Blackbird (*Agelaius phoeniceus*), and Ring-necked Pheasant (*Phasianus colchicus*), were recorded less frequently in mid-winter (i.e., in the second and third quarters) than at the beginning or end. Species observed on fewer than 5% of the censuses were not considered common enough to test for patterns of occurrence by winter quarter (Appendix).

DISCUSSION

Our study is the first of which we are aware that demonstrated significant effects of photoperiod, cumulative number of winter days, and weather components on bird species richness of upland and riparian forest birds in winter. The results appear to differ considerably from those of Robbins (1981a). He detected no effects of weather conditions on the numbers of selected species or families of birds from repeated coverage of a Winter Bird Survey route. Robbins' 8-km route in Maryland was covered at least three times per year for five consecutive years in late December or early January. He also analyzed data from eight years of Audubon Winter Bird-Population Studies on two forest plots in Maryland. There were no significant effects of temperature on the number of species he recorded. The differences between our results and those from Robbins may be due to (1) our larger sample size, (2) a longer season (i.e., November through February) in our study, (3) the fact that Robbins' (1981a) analyses were restricted to selected species and families, or (4) differences in location and climate. Most importantly, Robbins (1981a) selected for calm, dry mornings in both studies. Therefore, it is not surprising that he reported no weather effects on the number of species recorded.

Although ours is a long-term study, there were too few censuses to analyze the effects of number of winter days, photoperiod, and weather on species richness for specific winters. The data strongly suggest that differences in the detection of bird species occurred among winters. Previously, we (Stapanian et al. 1994) estimated extremely low seed crops for weeds, herbs, grasses, and bur oak for the winters of 1983–1984 and 1984–1985. Simi-

larly, we estimated extremely low weed seed and wild fleshy fruit crops for the winter of 1991–1992. These low food supplies may partly explain why the fewest species were recorded in those years. Large crops of herb and grass seeds were estimated for the winter of 1982–1983, which had relatively high values for species per station. Similarly, there were large crops of acorns and fleshy fruits for 1988–1989 and 1990–1991. In both winters, species richness was relatively high. These trends support the importance of the size of unrenewed food supplies in determining the detection of winter bird populations.

By treating the large winter differences as random effects, the statistical analysis demonstrated that photoperiod affects the morning activity of birds. The influences of photoperiodism on the physiology and activity of birds are well documented (Bissonette 1932, 1937; Bartholomew 1949; Welty and Baptista 1988 and references therein; Ball 1993; Hau et al. 1998). Perhaps when less time is available for feeding, as in mid-winter, birds spend less time in easily detected behaviors. The behavioral effect of reduced feeding time relative to energy needs is likely to be larger flock size (Caraco 1979, Sullivan 1988) and a lower probability of seeing birds at the average station.

Temperature and ground condition classes were significantly and negatively correlated ($r = -0.37$, $P < 0.001$, $n = 187$). Thus, what we perceived as difficult foraging conditions might have been simply a consequence of low temperature. Dew (ground condition class 2) and ground wet from rain or snowmelt (class 4) required that the air temperature exceed $0°$ C, while the temperature may be below $0°$ C for dry ground (class 1) and will be for frost (class 3). When we switched the number class of frost to 4 and rain or snowmelt to 3, the correlation coefficient between temperature and ground condition class increased in absolute magnitude ($r = -0.508$, $P < 0.001$). Ground condition may have little effect independent of temperature.

We are not sure how to interpret the negative effects of wind speed on bird species per census or bird species per station. Wind speed had a negative effect on both indicators of species richness even when we considered only those censuses in which wind speeds were less than 6.7 km/h, the speed above which wind chill temperature is less than air temperature. The effects of wind speed on species richness appear to be due to neither a decrease in our ability to hear birds, nor apparent additional thermoregulatory stress for the birds. However, wind speed typically increases after sunrise, and the wind speed at the end of a census may be greater than at the beginning. Small differences in wind speed at 07:00 may be magnified later in the census. There is evidence that some species, particularly those with small body sizes, can reduce metabolic demands in winter by selecting microhabitats that are sheltered from the wind and exposed to solar radiation (Wolf and Walsberg 1996).

Similarly, we are unsure why both indicators of species richness increased in later years. The same principal observer (C.C.S.) was present for all censuses in our study. Eyesight and hearing typically deteriorate over time (Cyr 1981), but these effects can be countered by individual experience with a specific route. The increases in species richness were not due to changes in mean annual temperature, because temperature and ordinal census year were not significantly correlated ($r = 0.109$, df $= 12$, $P > 0.05$). Wind speed on the census trips was negatively correlated with year and with both indicators of species richness. Thus, a decrease in wind speed on census days may partially explain the increases in species per station and species per census over the census years. Species composition on the census route changed over time. For example, the population of Carolina Wren (*Thryothorus ludovicianus*), a sedentary bird species, increased steadily during the 14 years of the census after a time when it was at low levels in the Manhattan Christmas bird counts. Wild Turkeys (*Meleagris gallopavo*) were reintroduced in the area in the early 1980s and their populations have increased since. These changes may be due to milder winters during the study period. There may have been an increase in canopy closure or structural diversity of the habitat on the route over the 14 years of the study, but that was not measured.

White-crowned Sparrows and White-throated Sparrows feed in large mixed flocks of sparrows in late winter and in smaller groups in late fall. These species were recorded on a

greater proportion of the censuses in the first quarter than in any other. November (first quarter) typically has the mildest average weather of any quarter and food abundance should be greatest at this time. Therefore, the selective pressure on birds for being in large flocks should be least at this time (Caraco 1979, Sullivan 1988). If members of a species were more widely distributed geographically, an observer would be more likely to record that bird species at least once on a census. Field Sparrows, Lincoln's Sparrows, and Common Grackles were also seen with greater frequency in November than in late winter. The Kansas Flint Hills are along the northernmost edge of the winter range of these three species (Thompson and Ely 1992). Although most members of these species migrate south out of the census area, a few overwinter (Zimmerman 1993). The decrease in numbers for these species during the winter could be a result of continued migration south or mortality in a marginal range.

The proportions of censuses on which Northern Bobwhite (a resident species), Golden-crowned Kinglet (a winter migrant), and Northern Flicker (winter resident and winter migrant; Thompson and Ely 1989, 1992; Zimmerman 1993) were recorded dropped steadily from the second through the fourth quarter. This decline may have been due to mortality to the wintering populations of those species. The results from our study for Golden-crowned Kinglet agreed with those of Zimmerman (1993) who hypothesized that the variation in departure of Golden-crowned Kinglets from the area was related to availability of food.

Eastern Meadowlark, Western Meadowlark, and Tufted Titmouse were recorded most frequently on censuses in the last quarter. These are resident species (Thompson and Ely 1992, Zimmerman 1993) that breed early in spring and begin establishing territories and/or obtaining mates in late winter. The American Tree Sparrow, a winter migrant to the area (Zimmerman 1993), was recorded least frequently in the first quarter. This agrees with Finck (1986), who found this species to be most numerous from December through February, suggesting a late migratory arrival. Red-winged Blackbird and Ring-necked Pheasant were most often recorded in November and February. These are resident or partly resident species that flock in severe weather in mid-winter. However, they begin preparation for breeding in late winter (Zimmerman 1993). Zimmerman (1993) found Red-winged Blackbird to be "occasional" during the winter months of most years in upland habitats until the migrants returned in late winter.

Our results are consistent with at least five hypotheses: (1) species are lost by mortality resulting from nonrenewed resources over the course of winter, (2) resident species move in and out of detection distance in the census area, (3) selective pressures for flock sizes change with weather conditions and food abundance, (4) some species are more easily detected in late winter because of early courtship behavior, and (5) species richness in the census area changes as a result of the arrival and departure of seasonally migrant species. The results suggest a complex relationship among weather components, photoperiod, abundance of resources, and species-specific evolutionary histories on winter bird species richness. We suggest further studies to analyze responses by individual species to resource abundance and abiotic factors in winter.

ACKNOWLEDGMENTS

LITERATURE CITED

ALTMAN, R. 1983. The effects of time of day on a winter bird survey. Ky. Warbler 59:23–26.

AXELROD, D. I. 1985. Rise of the grassland biome, Central North America. Bot. Rev. 51:163–201.

BALL, G. F. 1993. The neural integration of environmental information by seasonally breeding birds. Am. Zool. 33:185–199.

BARTHOLOMEW, G. A. 1949. The effect of light intensity and day length on reproduction in the English Sparrow. Bull. Mus. Comp. Zool. 101:433–476.

BISSONNETTE, T. H. 1932. Light and diet as factors in relation to sexual photoperiodicity. Nature (Lond.) 129:612.

BISSONNETTE, T. H. 1937. Photoperiodicity in birds. Wilson Bull. 49:241–270.

CARACO, T. 1979. Time budgeting and group size: a test of theory. Ecology 60:618–627.

COLLINS, P. T. 1989. Surviving the winter: the physiology of thermoregulation in birds. Passenger Pigeon 51:315–320.

CROWDER, M. J. AND D. J. HAND. 1990. Analysis of repeated measures. Monogr. Stat. Appl. Probability 41:1–257.

CYR, A. 1981. Limitation and variability in hearing ability in censusing birds. Stud. Avian Biol. 6: 327–333.

DAWSON, W. R. AND R. L. MARSH. 1986. Winter fattening in the American Goldfinch and the possible role of temperature in its regulation. Physiol. Zool. 59:357–368.

ERSKINE, A. J. 1992. A ten-year urban winter bird count in Sackville, New Brunswick. Can. Field-Nat. 106:499–506.

FINCK, E. J. 1986. Birds wintering on the Konza Prairie Research Natural Area. Proc. N. Am. Prairie Conf. 9:91–94.

HAU, M., M. WIKELSKI, AND J. C. WINGFIELD. 1998. A Neotropical bird can measure the slight changes in tropical photoperiod. Proc. R. Soc. London B 265:89–95.

HILDÉN, O. 1987. Finnish winter bird censuses: long-term trends in 1956–1984. Acta Oecol. 8:157–168.

HOUSTON, A. I. AND J. M. MCNAMARA. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. Ornis Scand. 24:205–219.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS systems for mixed models. SAS Institute, Inc., Cary, North Carolina.

LOERY, G. AND J. D. NICHOLS. 1985. Dynamics of a Black-capped Chickadee population, 1958–1983. Ecology 66:1195–1203.

PEACH, W. J., D. P. HODSON, AND J. A. FOWLER. 1992. Variation in the winter body mass of starlings *Sturnus vulgaris*. Bird Study 39:89–95.

PILASTRO, A., G. BERTORELLE, AND G. MARIN. 1995. Winter fattening strategies of two passerine species: environmental and social influences. J. Avian Biol. 26:25–32.

ROBBINS, C. S. 1972. An appraisal of the winter bird-population study technique. Am. Birds 26:1–4.

ROBBINS, C. S. 1981a. Bird activity levels related to weather. Stud. Avian Biol. 6:301–310.

ROBBINS, C. S. 1981b. Reappraisal of the winter bird-population study technique. Stud. Avian Biol. 6: 52–57.

ROBBINS, C. S., D. BYSTRAK, AND P. H. GEISSLER. 1986. The breeding bird survey: its first fifteen years, 1965–1979. Spec. Sci. Rep.-Wildl. 157:1–196.

ROGERS, C. M., V. NOLAN, JR., AND E. D. KETTERSON. 1994. Winter fattening in the Dark-eyed Junco: plasticity and possible interaction with migration trade-offs. Oecologia 97:526–532.

SAS INSTITUTE, INC. 1992. SAS/STAT software: changes and enhancements. Release 6.07. SAS Institute, Inc., Cary, North Carolina.

STAPANIAN, M. A. 1982. Evolution of fruiting strategies among fleshy-fruited plant species in eastern Kansas. Ecology 63:1422–1431.

STAPANIAN, M. A., C. C. SMITH, AND E. J. FINCK. 1994. Population variabilities of bird guilds in Kansas during fall and winter: weekly censuses versus Christmas bird counts. Condor 96:58–69.

SULLIVAN, K. A. 1988. Ontogeny of time budgets of Yellow-eyed Juncos: adaptation to ecological constraints. Ecology 69:118–124.

Thompson, M. C. and C. Ely. 1989. Birds in Kansas: vol. I. Univ. of Kansas, Univ. Press of Kansas, Lawrence.

THOMPSON, M. C. AND C. ELY. 1992. Birds in Kansas: vol. II. Univ. of Kansas, Univ. Press of Kansas, Lawrence.

U.S. NAVAL OBSERVATORY. 1945. Supplement to the American Ephemeris, 1946. Tables of sunrise, sunset, and twilight. U.S. Government Printing Office, Washington, D.C.

WAITE, T. A. 1992. Winter fattening in Gray Jays: seasonal, diurnal, and climatic correlates. Ornis Scand. 23:499–503.

WELTY, J. C. AND L. BAPTISTA. 1988. The life of birds, fourth ed. Saunders College Publishing, New York.

WHITE, C. M. AND G. C. WEST. 1977. The annual lipid cycle and feeding behavior of Alaskan Redpolls. Oecologia 27:227–238.

WOLF, B. O. AND G. E. WALSBERG. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. Ecology 77: 2228–2236.

ZIMMERMAN, J. L. 1993. The birds of Konza. Univ. Press of Kansas, Lawrence.

APPENDIX

The number of all censuses (All) and the mean proportion of censuses in 30-day intervals over 14 winters in which species were observed. For each species, we tested the null hypothesis that it was recorded in equal proportions in all four quarters. A *posteriori* tests (Tukey's pair-wise comparisons) were performed on those species for which the null hypothesis was rejected. Quarterly means for a species having the same letter were not significantly ($P < 0.05$) different. Species listed at the bottom lacked significant quarterly differences. Abbreviations: All = all censuses combined, n = number of censuses.

Common name	Scientific name	All $n = 194$	1–30 Nov $n = 52$	1–30 Dec $n = 42$	31 Dec–29 Jan $n = 46$	30 Jan–28 Feb $n = 54$
Northern Flicker	*Colaptes auratus*	171	0.962 A	0.986 A	0.873 AB	0.768 B
American Tree Sparrow	*Spizella arborea*	157	0.562 B	0.958 A	0.962 A	0.857 A
Tufted Titmouse	*Baeolophus bicolor*	153	0.673 B	0.642 B	0.902 A	0.929 A
Red-winged Blackbird	*Agelaius phoeniceus*	143	0.926 A	0.626 BC	0.579 C	0.831 AB
Western Meadowlark	*Sturnella neglecta*	99	0.576 AB	0.318 C	0.396 BC	0.737 A
Golden-crowned Kinglet	*Regulus satrapa*	84	0.604 A	0.669 A	0.321 B	0.127 B
Northern Bobwhite	*Colinus virginianus*	66	0.382 AB	0.461 A	0.364 AB	0.211 B
White-crowned Sparrow	*Zonotrichia leucophrys*	36	0.385 A	0.095 B	0.143 B	0.157 B
Ring-necked Pheasant	*Phasianus colchicus*	34	0.240 A	0.183 AB	0.014 B	0.294 A
Common Grackle	*Quiscalus quiscula*	24	0.308 A	0.060 B	0.024 B	0.071 B
Eastern Meadowlark	*Sturnella magna*	20	0.070 B	0.018 B	0.089 B	0.205 A
Field Sparrow	*Spizella pusilla*	18	0.270 A	0.071 B	0.056 B	0.032 B
White-throated Sparrow	*Zonotrichia albicollis*	14	0.173 A	0.060 AB	0.018 B	0.018 B
Lincoln's Sparrow	*Melospiza lincolnii*	13	0.130 A	0.065 AB	0.000 B	0.050 AB

American Crow (*Corvus brachyrhynchos*) 194, Black-capped Chickadee (*Poecile atricapillus*) 194, Dark-eyed Junco (*Junco hyemalis*) 193, Northern Cardinal (*Cardinalis cardinalis*) 192, House Sparrow (*Passer domesticus*) 192, Blue Jay (*Cyonocitta cristata*) 190, American Goldfinch (*Carduelis tristis*) 187, White-breasted Nuthatch (*Sitta carolinensis*) 187, Red-bellied Woodpecker (*Melanerpes carolinus*) 184, Downy Woodpecker (*Picoides pubescens*) 170, European Starling (*Sturnus vulgaris*) 169, American Robin (*Turdus migratorius*) 167, Red-tailed Hawk (*Buteo jamaicensis*) 157, Hairy Woodpecker (*Picoides villosus*) 143, Harris's Sparrow (*Zonotrichia querula*) 136, Eastern Bluebird (*Sialia sialis*) 128, Carolina Wren (*Thryothorus ludovicianus*) 97, Red-headed Woodpecker (*Melanerpes erythrocephalus*) 92, Rock Dove (*Columba livia*) 81, Song Sparrow (*Melospiza melodia*) 68, American Kestrel (*Falco sparverius*) 49, Brown Creeper (*Certhia americana*) 47, Northern Harrier (*Circus cyaneus*) 41, Cedar Waxwing (*Bombycilla cedrorum*) 40, Bewick's Wren (*Thryomanes bewickii*) 36, Spotted Towhee (*Pipilo maculatus*) 33, Wild Turkey (*Meleagris gollopavo*) 29, Mourning Dove (*Zenaido macroura*) 27, Pine Siskin (*Corduelis pinus*) 23, Brown-headed Cowbird (*Molothrus ater*) 20, Yellow-bellied Sapsucker (*Sphyrapicus varius*) 16, Winter Wren (*Troglodytes troglodytes*) 16, Sharp-shinned Hawk (*Accipiter striatus*) 14, Yellow-rumped Warbler (*Dendroica coronata*) 11, Loggerhead Shrike (*Lanius ludovicianus*) 7, Rough-legged Hawk (*Buteo lagopus*) 6, Horned Lark (*Eremophila alpestris*) 6, Rusty Blackbird (*Euphagus carolinus*) 6, Cooper's Hawk (*Accipiter cooperii*) 4, Purple Finch (*Carpodacus purpureus*) 3, Prairie Falcon (*Falco mexicanus*) 3, Fox Sparrow (*Passerella iliaca*) 3, Sedge Wren (*Cistothorus platensis*) 2, Red-breasted Nuthatch (*Sitta canadensis*) 2, Brown Thrasher (*Toxostoma rufum*) 2, Hermit Thrush (*Catharus guttatus*) 1, Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) 1.